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06 September 2017

Version of attached file:

Accepted Version

Peer-review status of attached file:

Peer-reviewed

Citation for published item:

Gkafas, G.A. and Exadactylos, A. and Rogan, E. and Raga, J.A. and Reid, R. and Hoelzel, A.R. (2017) 'Biogeography and temporal progression during the evolution of striped dolphin population structure in European waters.', *Journal of biogeography*, 44 (12). pp. 2681-2691.

Further information on publisher's website:

<https://doi.org/10.1111/jbi.13079>

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1 Original Article

2 **Biogeography and temporal progression during the evolution of striped dolphin population**
3 **structure in European waters**

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18 **Running title:** Population structure of striped dolphin in European waters

19

20 **Word count of abstract + main text + references:** 6987

21 **Figures & Tables:** Approximately 1.5 pages

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23

24

25 **Abstract**

26 **Aim**

27 We investigated the population genetic structure of a highly mobile marine species, the striped
28 dolphin, *Stenella coeruleoalba* (Meyen, 1833), along a geographic range with habitat transitions
29 and historical dynamics to identify the causes of genetic divergence, and to assess the effect of past
30 climate change on demography and population connectivity.

31 **Location**

32 North-east Atlantic Ocean and Mediterranean Sea.

33 **Methods**

34 Twenty microsatellite loci were used in conjunction with coalescent methods to investigate the
35 genetic structure and demographic history of striped dolphins (*Stenella coeruleoalba*) in the
36 Mediterranean Sea and eastern North Atlantic Ocean. Approximate Bayesian modelling was used to
37 compare the support for alternative scenarios for the pattern of divergence over time in the context
38 of known geographic transitions and environmental change over the course of the Quaternary.

39 **Results**

40 We describe a novel pattern of structure among the extant populations along north/south and
41 east/west axes. Modern gene flow shows strong directionality from north-east to south and west in
42 the North Atlantic, and from west to east in the Mediterranean. On a temporal scale we found
43 evidence for a progression starting with a division between the North Atlantic and Mediterranean
44 Sea populations during the middle Pleistocene, followed by a division within the Mediterranean
45 between the east and west basins towards the end of the Pleistocene, and finally an east/west
46 division in the eastern North Atlantic at the start of the Holocene.

47 **Main conclusions**

48 In the context of known population structure for other marine species along the same geographic
49 range, our data facilitate inference of the more general processes that shaped patterns of
50 biogeography across this region through the environmental transitions of the Quaternary. In
51 particular, Pleistocene era divisions apparently reflect strong physical habitat boundaries, with later
52 divisions associated with climate warming in the Holocene.

53

54 Key words: Holocene, Mediterranean Sea, migration, North Atlantic Ocean, Pleistocene, population
55 structure, *Stenella coeruleoalba*

56

57 **Introduction**

58 Species biogeography is shaped by demographic processes through evolutionary and
59 ecological time-scales, including influence from environmental instability and/or direct
60 anthropogenic pressures. Alterations in species ecological niches can influence their demographic
61 history, adaptation and dispersal behaviour. It is well known that climatic oscillations in the
62 Quaternary were responsible for significant changes in species distributions and population
63 dynamics in terrestrial environments (e.g. see Hewitt 2004). In marine systems genetic breaks (e.g.
64 Barber *et al.* 2000) and recolonization through migration (e.g. Wares & Cunningham 2001)
65 contributed to altering genetic structure among populations throughout the Quaternary period.
66 During Pleistocene glaciations, sea level was reduced and environmental conditions were re-
67 distributed sometimes creating isolated refugia, imposing at first geographical barriers to gene flow
68 followed by post glacial dispersal and expansion (Xue *et al.* 2014). This has been reported for
69 various fish species (e.g. Bargelloni *et al.* 2005), and this pattern of vicariance followed by re-

70 colonization of marine organisms, often associated with bottlenecks and expansions, likely shaped
71 contemporary genetic structure for various species.

72 Marine mammals have reportedly experienced declines during the last Last Glacial
73 Maximum (LGM; see de Bruyn *et al.* 2011; Moura *et al.* 2014), subsequent re-expansion (e.g.
74 Banguera *et al.* 2010) and species-specific effects associated with habitat release and loss (e.g. de
75 Bruyn *et al.* 2009). For example, studies report that modern harbour porpoise (*Phocoena phocoena*)
76 populations in the eastern North Atlantic and North Sea have evolved during the late Pleistocene
77 (Martinez-Bakker *et al.* 2013) or early Holocene (see Fontaine *et al.* 2014), including phenotypic
78 adaptation and differential prey choice suited to different habitats (de Luna Lopez *et al.* 2012,
79 Fontaine *et al.* 2014). A similar effect was suggested for *Lagenorhynchus* species in the North
80 Atlantic (Banguera *et al.* 2014).

81 Across the geographic range extending from the Black Sea through the Mediterranean Sea
82 and through the eastern North Atlantic to Scotland, studies have proposed habitat-related barriers to
83 gene flow for harbour porpoise (Fontaine *et al.* 2014) and bottlenose dolphins (Natoli *et al.* 2005).
84 In the bottlenose dolphin study there was differentiation across established oceanographic
85 discontinuities (such as the Almeria Oran front; Tintoré *et al.* 1988) that had shown evidence for
86 restricting gene flow for a diversity of marine species (see Natoli *et al.* 2005). This includes various
87 fish species such as *Solea solea* (Exadactylos *et al.* 1998), *Solea vulgaris* (Guarniero *et al.* 2002),
88 *Dicentrarchus labrax* (Bahri-Sfar *et al.* 2000) and the bivalve *Mytilus galloprovincialis* (Quesada *et*
89 *al.* 1995). In contrast, common dolphins (*Delphinus delphis*) show little or no population structure
90 through a similar range (e.g. Mirimin *et al.* 2009), and the fine scale structure shown (between the
91 eastern and western basins of the Mediterranean Sea; e.g. Natoli *et al.* 2006) may be driven by
92 relatively recent processes associated with anthropogenic impact (Moura *et al.* 2013a). Social
93 coherence within local populations may be an ancillary mechanism promoting philopatry and
94 habitat dependence, as in the extreme case of the killer whale (*Orcinus orca*), where social cohesion

95 in kin-groups is strong enough to largely define regional population structure in this species
96 (Hoelzel *et al.* 2007; Pilot *et al.* 2010). Social kinship associations have been investigated in other
97 delphinid species, including the striped dolphin (*Stenella coeruleoalba* (Meyen, 1833)), and a
98 significant association among adult female kin in small social groups was reported (Gaspari *et al.*
99 2007).

100 Here we investigate the processes promoting population structure using data from the same
101 eastern North Atlantic and Mediterranean geographic range for the striped dolphin. The striped
102 dolphin is distributed world-wide in tropical and temperate waters (see Hammond *et al.* 2008). In
103 the Mediterranean Sea it is the most common and abundant species (Notarbartolo di Sciara *et al.*
104 1993). Among earlier studies Galov *et al.* (2009) reported a lack of genetic differentiation for
105 striped dolphin mtDNA control region haplotypes between the Croatian part of the Adriatic Sea and
106 the rest of Mediterranean Sea. Another mtDNA study showed no subdivision within the broader
107 Mediterranean Sea (Garcia-Martinez *et al.* 1999). However microsatellite DNA revealed genetic
108 differentiation between the Mediterranean Sea and North Atlantic (Bourret *et al.* 2007; Gaspari *et*
109 *al.* 2007), between the western and eastern Mediterranean basins, and a weak pattern of isolation by
110 distance between nearshore and offshore populations in the Ligurian Sea (Gaspari *et al.* 2007).
111 However, these studies were based on relatively few samples, few loci (up to 8) and limited
112 geographic range.

113 To test our hypotheses about historical biogeography we required greater resolution and a
114 broader sampling range. We use these data to undertake demographic modelling using the
115 approximate Bayesian computational (ABC) method, permitting novel inference. We use fine-scale
116 sampling to test the hypothesis that the point of division between the western and eastern
117 Mediterranean basins is across the Sicily channel as proposed for other species (e.g. Guarniero *et al.*
118 2002 for common sole, *Solea vulgaris*; Natoli *et al.* 2005 for bottlenose dolphins). We use
119 historical modelling to test hypotheses about the pattern and timing of population founding and

120 divisions in the context of Quaternary environmental change. In particular, we consider the
121 potential impact of periods of sea-level change during Pleistocene glaciations and the impact of
122 warming during the Holocene.

123

124 **Material and Methods**

125 **Samples collection and Study area**

126 Striped dolphin samples were collected from strandings and fisheries bycatch from the
127 Mediterranean Sea and the eastern North Atlantic Ocean. Sampling sites and sizes are shown in Fig.
128 1. The total sample size was 256, and all used in this study for the first time. Tissue samples were
129 either stored in 20% DMSO NaCl 5M or in 70% ethanol. The majority of the stranded individuals
130 from the western Mediterranean died during a morbillivirus epizootic during 1990-1992 and 2006-
131 2008. However, further stranded samples from the same region were collected from 1989 and
132 during 1993-2005 for which the cause of death is unknown. Overall 36 samples were collected
133 between 1990 and 1992 and 21 between 2006 and 2008 from this region.

134 **DNA extraction and PCR amplification**

135 Skin and muscle tissue were extracted following a standard phenol/chloroform extraction
136 protocol (after Hoelzel 2009). A panel of 29 microsatellite DNA loci were tested (see Table S1 in
137 Appendix S1 in Supporting Information). A multiplex PCR Kit (Qiagen) with hot start Taq was
138 used for the DNA amplifications. The 29 pairs of primers were divided into 4 multiplex Groups
139 (Table S1 in Appendix S1) according to size range and florescent primer pigment. The PCR cycling
140 profile was: 95°C for 15 minutes; 30 cycles of 95°C for 1 minute, annealing temperature for 30
141 seconds and 72°C for 30 seconds; 72°C for 15 minutes. PCR products were verified by agarose gel

142 electrophoresis. Amplified DNA products were screened on an ABI 3730 DNA Analyser (Applied
143 Biosystems) using the ROX500 size marker. Each specimen's alleles were scored by the software
144 STRAND 2.0 (Toonen & Hughes 2001) and 10% of genotypes were redone for error checking.

145 **Statistical analysis**

146 All loci were tested for the presence of null alleles or allelic dropout using the software
147 MICROCHECKER 2.2.3 (van Oosterhout *et al.* 2004). Exact tests for Hardy-Weinberg equilibrium
148 and Linkage Disequilibrium (using the Markov Chain Monte Carlo (MCMC) method with 10,000
149 dememorization steps followed 1,000 batches with 10,000 iterations per batch), were carried out
150 using GENEPOP 3.4 (Raymond & Rousset 1995). BAYESCAN (Foll & Gaggiotti 2008) was used to
151 identify candidate loci under natural selection, running 100,000 iterations. Expected heterozygosity
152 (H_{EXP}) and observed heterozygosity (H_{OBS}) were estimated using GENEPOP 3.4 (Raymond &
153 Rousset 1995). Fixation indexes F_{ST} and F_{IS} , using the formulations described by Weir &
154 Cockerham (1984; significance tested using 10,000 permutations test) and the number of alleles per
155 locus were calculated using ARLEQUIN 3.5 (Excoffier & Lischer 2010).

156 Factorial correspondence analysis (FCA) was performed using GENETIX 4.05.2 (Belkhir *et*
157 *al.* 2002) and the '3D by populations' setting. Population structure was further assessed using
158 STRUCTURE 2.3 (Pritchard *et al.* 2000) assuming correlated allele frequencies and admixture. Three
159 independent repeats were run for each value of K ($1 \leq K \leq 10$). Following test runs, the burn-in
160 length and length of simulation were set at 1,000,000 and 3,000,000 repetitions, respectively.
161 STRUCTURE HARVESTER was used to assess the likelihood value of the different K values and to
162 implement the ΔK method (Evanno *et al.* 2005) reflecting the highest hierarchical level of
163 structuring (Earl & von Holdt 2012).

164 A hierarchical analysis of molecular variance (AMOVA; Excoffier & Lischer 2010) was
165 performed to partition variance components attributable to (1) variance between areas (the North
166 Atlantic and the Mediterranean); (2) variance between populations within areas; (3) variance among
167 samples within populations; and (4) within individuals. The significance of the resulting F -indices
168 was considered after sequential Bonferroni correction and variance components were permuted
169 10,000 times. Evidence of bottleneck signatures was assessed using BOTTLENECK (Cornuet &
170 Luikart 1996) with significance tests done for the infinite allele, two parameter and stepwise
171 mutation models (1,000 iterations; TPM model was used with default settings of 70% variation
172 from the SMM model and 30% from the IAM model). The Garza-Williamson M -ratio test was
173 implemented to test a bottleneck signal using the software ARLEQUIN 3.5 (Excoffier & Lischer
174 2010). Bottleneck analyses were not undertaken for the Biscay Gulf population due to the relatively
175 small number of samples. BAYESASS 3.0 (Wilson & Rannala 2003) was used to infer the rates and
176 directionality of contemporary migration. In order to achieve acceptance ratios between 20%-60%
177 values of Δ_M , Δ_A and Δ_F were set to 0.10, 0.30 and 0.50, respectively using 3×10^6 iterations and a
178 burn-in of 10^6 . The software TRACER 1.6 was used (Rambaut & Drummond 2007) to check for
179 convergence.

180 To compare demographic scenarios of divergence history, an approximate Bayesian
181 computational analysis was implemented in the software DIYABC 2.0.3 (Cornuet *et al.* 2008).
182 Different scenarios about population history were compared and their relative support assessed
183 using direct and logistic regression analyses. Scotland, Ireland, the western Mediterranean
184 (Gibraltar strait, Valencia, Strait of Sicily and Ionian Sea) and the eastern Mediterranean
185 (Korinthiakos Gulf and Israel) basins were pooled (according to FCA results, see below) and
186 compared. The Biscay Gulf sample was relatively small and differentiated from Scotland and
187 Ireland, and so not included in this analysis. Broad log-normal priors were used (see Table 1) and
188 multiple scenarios were tested considering alternative division times and demographics. We first

189 test 10 unique permutations varying the number of time division points (2, 3 or 4), the identity of
190 the ancestral population and the identity of populations dividing at different time points. This
191 covered the main alternatives, but was not exhaustive, and so in a second analysis we retain the
192 basic case where all split at the same time, the best supported scenarios from the first run, and add
193 some scenarios that consider plausible alternative patterns of ancestry (for a total of 12 scenarios;
194 see Fig. S1 in Appendix S2 in Supporting Information). 1.2×10^7 data sets were implemented for
195 each scenario. The best fit was obtained by direct and logistic regressions of each scenario. Given a
196 best supported scenario, we then assessed the probability of the deviation between simulated and
197 observed summary statistics for the number of alleles, gene diversity and F_{ST} .

198

199 **Results**

200 Among the 29 loci screened, only one locus showed evidence of null alleles (TexVet 5) and
201 two of them could not be amplified for the entire data set (D08, Dde59), therefore 26 loci were
202 used for the statistical analyses. These 26 loci were tested for Hardy-Weinberg equilibrium (HWE)
203 and at four loci (KWM1b, MK3, Sco28 and Sco66) significant departures were detected in multiple
204 populations (after Bonferroni correction, Rice 1989). There was no significant linkage
205 disequilibrium. Furthermore, two loci (Ev37 and Sco11) showed evidence for positive selection
206 from the assessment of outliers in BAYESCAN. Thus, a final set of 20 loci were used for further
207 analyses. Replicate genotyping detected no differences and so no error rate based on those data.
208 Missing data are illustrated in Table S2 in Appendix S1.

209 The scatter plot of FCA (Fig. 2) showed clear differentiation between Mediterranean Sea and
210 eastern North Atlantic Ocean populations. Within the Mediterranean Sea basin, populations were
211 divided into two separate groups (Fig. 1). Based on the FCA data, samples from GS, VL, SS and IS
212 were clustered as western Mediterranean (WM), whereas samples from KG and IS were clustered
213 as eastern Mediterranean (EM). The apparent boundary is east of the commonly proposed position

214 at the Strait of Sicily (e.g. Exadactylos *et al.* 1998). In the North Atlantic there is a weaker
215 division, roughly on an east/west axis (see Fig. 2; note that the division lines are only illustrative).
216 Comparing individual samples by collection date showed that this had no impact on the pattern of
217 structure shown in the FCA analysis (Fig. S2 in Appendix S2). Genetic variation at each locus for
218 each population is reported in Table S3 in Appendix S1 (including H_o , H_e , F_{IS} , number of alleles
219 and allelic richness). All pairwise F_{ST} values were significant and highest for comparisons between
220 the North Atlantic and Mediterranean Sea (Table 2).

221 For the analysis in STRUCTURE, $\text{LnP}(K)$ leveled off after $K=2$ (Fig. S3 in Appendix S2), and
222 $\Delta K = 2$. At $K = 2$, the two clusters separate the North Atlantic and the Mediterranean Sea (Fig. S3A
223 and Fig. S4A in Appendix S2). Independent analyses for each of these two clusters gave a
224 maximum $\text{LnP}(K)$ for the North Atlantic samples of $\Delta K = 2$ (Fig. S3B and Fig. S4B in Appendix
225 S2) and for the Mediterranean samples $\Delta K = 3$ (Fig. S3C and Fig. S4C in Appendix S2). However,
226 the trend for $\text{LnP}(K)$ showed little change between $K=1-3$ for either within region comparison, and
227 so the support for $K>1$ is not strong for those analyses (see Fig. S3 in Appendix S2). The
228 hierarchical AMOVA found significant support for differentiation both between the two main
229 groups (North Atlantic versus the Mediterranean Sea) and among populations within groups (Table
230 S4 in Appendix S1), consistent with the results found by FCA and STRUCTURE.

231 The program BOTTLENECK did not show statistical support for a bottleneck event in any of the
232 North Atlantic regions based on heterozygote excess (Table S5 in Appendix S1) or the allele
233 frequencies mode shift as the distribution was clearly L shaped as expected for non- bottleneck
234 populations close to mutation-drift equilibrium (Fig. S4 in Appendix S2). The Garza-Williamson
235 M -ratio index for Scotland ($M=0.836 \pm 0.152$) and Ireland ($M=0.893 \pm 0.107$) were both over the
236 suggested threshold of 0.68 identified by Garza & Williamson (2001). Within the Mediterranean
237 basin BOTTLENECK gave significant evidence for bottleneck events, but only when applying the

238 stepwise mutation model (Table S5 in Appendix S1). However, *M-ratio* did not reveal any evidence
239 for bottleneck events within the Mediterranean basin (WestMed: 0.823 ± 0.165 , EastMed: $0.733 \pm$
240 0.174).

241 Estimates for contemporary rates and patterns of gene flow (based on BayesAss) are provided
242 for comparisons among five putative populations: Scotland, Ireland, the Biscay Gulf, the western
243 Mediterranean, and the eastern Mediterranean (Tables 3, S6 in Appendix S1, Fig. 3). There was a
244 strong indication of directionality from the north (Scotland) into populations to the west (Ireland)
245 and south (Biscay Gulf), and from the western into the eastern Mediterranean Sea.

246 The initial comparison of 10 scenarios in the DIY-ABC analysis (Fig. S1a in Appendix S2)
247 revealed that scenario 8 best fits the observed data (Fig. 4). This scenario was also the best fit
248 among the 12 scenarios illustrated in Fig. S1b in Appendix S2. Details of the relative support from
249 logistic and direct regression analyses together with confidence intervals are provided in Table S6
250 in Appendix S1. The best supported scenario has much greater support than the tested alternatives
251 (Fig. 4; Table S7 and Table S8 in Appendix S1), and is based on the hypothesis of a common
252 ancestor (with effective size N_a ; Table 1) that was split into Mediterranean and Atlantic Ocean
253 populations (at t_3), followed by divergence within the Mediterranean Sea (t_2), and a more recent
254 divergence within the Atlantic Ocean (t_1 ; Fig. 4). Posterior support for parameter estimates are
255 illustrated in Fig. S6 in Appendix S2 and presented in Table 1. The time of the first divergence
256 event (t_3) was estimated at a median of 34,700 generations ago. The estimated generation time by
257 Taylor *et al.* (2007) of 22 years for the striped dolphin, would imply this divergence occurring
258 approximately 763 Ka during the middle Pleistocene. Following that, the Mediterranean basin
259 divergence occurred approximately 53 ka (t_2) during Late Pleistocene while divergence within the
260 Atlantic Ocean occurred approximately 6 ka (t_1) at the start of the Holocene. Effective population

size estimates suggest that Scotland and the eastern Mediterranean are smallest, and that the ancestral population size was relatively small (Table 1).

Discussion

The evolution of population structure can be influenced by both biotic and abiotic factors. Biotic interactions may be driven by competition or other frequency dependent factors that can influence patterns of diversity. Changes in environmental factors (e.g. climatic or oceanographic) may also drive patterns of diversity, and the relative contribution of biotic and abiotic factors has been discussed at some length (see Benton 2009). Our results provide chronological data that may help provide inference in this context. Environmental change over time can lead to diversification shifts (Perry *et al.* 2005) and phylogeographic breaks (Avice 2000). One well established mechanism is through climatic change, especially over the Pleistocene glacial cycles (e.g. Hewitt 2004). Perhaps at the same time competition over resources can lead to differential resource specialisation and habitat dependence, promoting divergence across habitat boundaries (e.g. Natoli *et al.* 2005). The marine environment across the geographic range from the Mediterranean Sea to the North Sea, along the southern and western coastline of Europe, is characterised by a number of transitions, and these have been dynamic in nature over time. There are boundaries that are known to be associated with reduced gene flow for a diversity of extant species (e.g. Limborg *et al.* 2012), however not all species show the same pattern.

There are seven putative phylogeographic breaks (likely including varying transition ranges and extents) from the Mediterranean Sea to the North Atlantic where barriers to gene flow have been reported for various taxa. Between the North Atlantic and the Mediterranean Sea there are putative breaks at the Strait of Gibraltar and the Almeria-Oran front (e.g. Bahri-Sfar *et al.* 2000; Guarniero *et al.* 2002; Gaspari *et al.* 2007). Within the Mediterranean Sea there are three breaks: the Dardanelle Strait which separates the Black Sea and Mediterranean Sea (e.g. Nikula & Vainola

286 2003), the boundary between the Adriatic Sea and Mediterranean Sea (e.g. Galov *et al.* 2009), and
287 the Italian Peninsula separating the eastern and western Mediterranean basins (e.g. Natoli *et al.*
288 2006; Rolland *et al.* 2007). In the North Atlantic between the Mediterranean and the North Sea
289 there are at least two breaks: the barrier between the Biscay Gulf and the English Channel (Jolly *et*
290 *al.* 2005; Fontaine *et al.* 2014) and in the Skagerrak between the North Sea and the Baltic Sea (e.g.
291 Johannesson & Andre 2006). Not many species have been studied across all or most of these
292 regions, but a direct comparison can be made between the common dolphin which showed
293 panmixia across most of the range (Natoli *et al.* 2006; Mirimin *et al.*, 2009; Moura *et al.* 2013a) and
294 the bottlenose dolphin which showed differentiation across nearly all of these boundaries (Natoli *et*
295 *al.* 2005; Louis *et al.* 2014).

296 Our data for the striped dolphin show a north/south and east/west dimension to the pattern
297 of population structure. However, there are also indications of dynamic interactions over the course
298 of the Pleistocene, such that the earliest division (middle Pleistocene) is between the North Atlantic
299 and the Mediterranean, the next division (late Pleistocene) is between the eastern and western
300 Mediterranean, and finally between the population around Scotland and those further south and
301 west (at around the start of the Holocene). Evidence for striped dolphin population expansion
302 through the Pleistocene was provided from the Ne estimates in the ABC analyses, since the ancestor
303 value was lower than for all extant estimates (Table 1). During the Pleistocene epoch, oscillations
304 such as changes in sea level, upwelling events, temperature alterations and changes in the
305 distribution of food resources may have played a role in the changing dynamics of delphinid
306 populations (see Banguera *et al.* 2010; Moura *et al.* 2014). Sea level during glacial periods within
307 the Pleistocene is estimated to have dropped by about 110 to 120 metres (Lambeck *et al.* 2005)
308 which may have influenced population dynamics, dispersion and colonization in the Mediterranean
309 basin. This could have promoted vicariance between the North Atlantic and the Mediterranean

310 basins early on, and perhaps between the separate basins of the Mediterranean after that (as
311 suggested by our analyses).

312 After the LGM, rapid warming affected the nature and availability of coastal marine habits.
313 According to Boehme *et al.* (2012) investigating habitat suitability for grey seals (*Halichoerus*
314 *grypus*), during the LGM the higher latitudes of the North Atlantic Ocean were isolated, and only
315 the Biscay Gulf and Iberian Peninsula were suitable for habitation. Our data suggest that population
316 differentiation was generated in this region following the LGM, and a post-glacial expansion
317 associated with population structuring in the eastern North Atlantic has been discussed for other
318 marine mammals (Banugera *et al.* 2010; 2014; Fontaine *et al.*, 2014). Of course earlier glacial/
319 inter-glacial transitions during the Pleistocene Milankovitch cycles may have had the potential to
320 generate structure in this region as well. It is possible that we are detecting the latest phase of what
321 may have been a period of reticulation as populations in this region divided and re-formed.

322 The pattern of contemporary population structure detected was consistent for the FCA,
323 STRUCTURE, BAYESASS analyses and measures based on summary statistics. There was division
324 between the Mediterranean and North Atlantic, as seen for a broad range of species from
325 invertebrates to fin whales (e.g. Quesada *et al.* 1995; Berube *et al.* 1998). The structure in the
326 North Atlantic was more unusual. Here the magnitude of differentiation was less, though detectable,
327 highly directional (with contemporary gene flow out of Scotland for the most part), and showed
328 division both east to west (between Scotland and Ireland) and north to south (between Scotland and
329 the Biscay Gulf). Scotland is near the northern range limit for the striped dolphin, which may
330 explain a tendency for gene flow to the south, despite recent warming from anthropogenic climate
331 change. Previous studies on microsatellite loci (Bourret *et al.* 2007) and mtDNA (Garcia-Martinez
332 *et al.* 1999) did not reveal any differences among striped dolphin populations in this region of the
333 Atlantic Ocean, however each provided a lower level of resolution than reported here. While other

334 studies have described relatively fine-scale differentiation in this region for other marine mammals
335 (Natoli *et al.* 2005; Fontaine *et al.* 2014) and fishes (Exadactylos *et al.* 1998), differentiation is
336 more typically between northern and southern populations rather than east to west.

337 In the Mediterranean Sea, Gaspari *et al.* (2007) found significant differentiation between
338 striped dolphin populations sampled from Spain (Balearic Sea) and those from the west of Italy
339 (Ligurian Sea). A finer scale diversity pattern was also recorded between samples from the eastern
340 north side of Italy (Croatia, Puglia, Greece) and the western side of Italy (Ligurian Sea and
341 Tuscany). Our data suggest a division to the east of Sicily, between the Ionian Sea and Greece,
342 though perhaps affected by post-mortem drift in currents. However, the Korinthiakos Gulf in
343 Greece is semi-enclosed and consists of a unique water body due to deep and steep slopes along its
344 coasts, and a systematic occurrence of wind-driven upwelling currents (Lascaratos *et al.* 1989).
345 Although waters from the Ionian Sea enter the gulf, overall it provides an isolated habitat. Frantzis
346 & Herzing (2002) in a study of delphinid species sightings and abundance in Korinthiakos Gulf
347 suggested philopatry of striped dolphins there. The eastern Mediterranean basin consists of the
348 Ionian, Aegean and Levantine Seas, which are dynamically active areas with unique oceanographic
349 features and different water masses compared to the western Mediterranean basin (Theocharis *et al.*
350 1993). Different patterns of water circulation and different mass exchanges such as low salinity out-
351 flow from the Black Sea, in conjunction with the freshwater input of the continental shelf, and the
352 high salinity input from the Levantine Sea and Ionian Sea, create complex cyclonic and anticyclonic
353 gyres (e.g. Kourafalou *et al.* 2004). These different systems contribute to differentiated nutrient-
354 enriched water masses, supporting different food resources and availability (Theodorou 2004). The
355 region represents a transition zone with respect to ecological niches for many marine species (e.g.
356 Viñas *et al.* 2010). Therefore subtle differences in habitat structure may be expected, and the
357 boundary point suggested by our data could be more than an artefact. This could be resolved
358 through the collection of samples from free-ranging animals in the region.

359 There are now data on population genetic structure for three delphinid species across the full
360 geographic range from the eastern Mediterranean to Scottish waters. Common dolphins stand out
361 as distinct showing panmixia (Moura *et al.* 2013a), even though this species shows fine-scale
362 population structure in the Pacific (e.g. Bilgmann *et al.* 2008). The striped dolphin shows a pattern
363 of structure that is more similar to that seen for the bottlenose dolphin (Natoli *et al.* 2005; Louis *et*
364 *al.* 2014), but these two species also differ. For effective conservation and management,
365 understanding what drives these differences is critical, since it will often be necessary to base
366 strategy on transferable inference. Given the numbers, it is impractical to instead investigate all
367 species of concern individually in all regions of conservation concern. This particular geographic
368 region provides a useful study system due to the complexity and known phylogeographic breaks
369 (shared by a range of different species). While the bottlenose dolphin apparently shows
370 differentiation across expected habitat boundaries throughout this range (Natoli *et al.* 2005), the
371 striped dolphin shows differentiation at some of the same boundaries, though not in exactly the
372 same way. Data on the historical context helps us understand the process of differentiation, and the
373 relative roles that biotic and abiotic factors may have played for each of these species.

374 A comparison based on mitogenome sequences between populations at either extreme of the
375 geographic range (between Scotland and the eastern Mediterranean) suggests relatively recent
376 radiation among bottlenose dolphin populations (Moura *et al.* 2013b), during the late Pleistocene.
377 This may be consistent with processes associated with local habitat dependence and differential
378 resource specialisation. In contrast, our data for the striped dolphin suggest a division between the
379 North Atlantic and Mediterranean in the middle Pleistocene, perhaps instead associated with
380 climate change and vicariance events. Boundaries established by abiotic factors may be reinforced
381 by habitat dependence and competition, and the details of the division for the striped dolphin within
382 the Mediterranean suggest that this may be the case, especially if the boundary is displaced
383 eastward from that seen for the bottlenose dolphin. In general, habitat boundaries appear to establish

384 divisions early on, while the more recent division in the North Atlantic may have been in response
385 to warming climate at the start of the Holocene.

386

387 **Conflict of Interest**

388 The authors declare no conflict of interest.

389

390 **Acknowledgements**

391 We thank Dr S. Gaspari (University of Florence, Florence, Italy), Willy Dabin (University of La-
392 Rochelle, La-Rochelle, France), Vasilis Podiadis (Multihull Yachting Greece, Lavrio, Hellas) for
393 providing us with samples from Ionian Sea, Biscay Gulf, Scotland, Israel, Strait of Gibraltar and
394 Strait of Sicily. Samples in Ireland from stranded animals were collected via funding from a number
395 of sources and we gratefully acknowledge The Heritage Council of Ireland; European Commission
396 ECFAIR contract FAIR-CT95-0523: Assessment and Reduction of the By-catch of Small
397 Cetaceans of Small Cetaceans (BY-CARE); contract EVK3-2000-00027: Bioaccumulation of
398 persistent organic pollutants in small cetaceans in European waters: transport pathways and impact
399 on reproduction (BIOCET). Sampling along the Valencian coast has been supported by Conselleria
400 de Medio Ambiente and Conselleria de Educación (PROMETEOII/2015/018) of the Generalitat
401 Valenciana. This study was funded by the Hellenic State Scholarship Foundation through PhD
402 grant awarded to Dr Georgios A. Gkafas. We thank Andrew Brownlow for helpful comments on
403 the manuscript.

404

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Data accessibility

Genotype data is archived on a Dryad database; xxx

Supporting Information

Appendix S1: Tabulated molecular genetic data

Appendix S2: Further illustrations

Biosketch

George A. Gkafas is a molecular evolutionary biologist working as a post-doctoral researcher at the University of Thessaly, Greece, and a past and recent member of the Molecular Ecology Group

683 at Durham University, UK, which focuses on understanding the evolution of biodiversity and the
684 historical context of biogeography for a wide range of study species.

685
686 Author contributions: study was conceived by ARH and GAG and the analyses undertaken mostly
687 by GAG. The paper was written by GAG and ARH with feedback from all co-authors. Samples
688 and data on regional populations were provided by ER, JAR and AE.

689
690 **Handling Editor**
691 Michelle Gaither

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697 **Table 1** Prior distribution settings and parameter estimates (Mode and Median) for the DIY-ABC
698 analyses, using 1.2×10^7 data sets simulated under scenario 8 (95% confidence intervals are shown
699 for each of the parameters) for striped dolphin populations.

Parameter	Prior range	Mode	Median	95% CI low	95% CI high
<i>N1</i> (Scotland)	10 - 10^7	1,480	12,900	644	274,000
<i>N2</i> (Ireland)	10 - 10^7	71,400	769,000	44,100	8,240,000
<i>N3</i> (W Med)	10 - 10^7	14,200	34,000	5,340	700,000
<i>N4</i> (E Med)	10 - 10^7	204,000	10,200	539	147,000
<i>Na</i> (Ancestral)	10 - 10^5	10	64	10	2,030
<i>t0</i> (generations)	10 - 10^4	1	26.2	1	611
<i>t1</i> (generations)	10 - 10^5	44.1	273	17.4	3,160
<i>t2</i> (generations)	10 - 10^6	248	2,410	107	8,690
<i>t3</i> (generations)	10 - 2×10^6	24,400	34,700	6,250	127,000

702 **Table 2** F_{ST} pairwise values of the striped dolphin populations. An asterisk indicates significance, with
703 alpha set to 0.05 after Bonferroni correction.

	Scotland	Ireland	Biscay Gulf	western Mediterranean	eastern Mediterranean
Scotland	0				
Ireland	0.012*	0			
Biscay Gulf	0.012*	0.010*	0		
western Mediterranean	0.045*	0.033*	0.044*	0	
eastern Mediterranean	0.051*	0.053*	0.056*	0.032*	0

707 **Table 3** Contemporary migration rates (\pm sd) of the striped dolphin populations as derived using the
708 BAYESASS software (confidence intervals are given in parentheses). Values are given as m , the
709 proportion of migrants per generation from each population on the left (row headings) into the
710 populations on the right (column headings).

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	Scotland	Ireland	Biscay Gulf	western Mediterranean	eastern Mediterranean
Scotland	-	0.297 ± 0.015 (0.267 - 0.326)	0.249 ± 0.032 (0.186 - 0.312)	0.017 ± 0.007 (0.003 - 0.184)	0.041 ± 0.019 (0.004 - 0.078)
Ireland	0.06 ± 0.006 (0.012 - 0.072)	-	0.035 ± 0.023 (0.001 - 0.08)	0.003 ± 0.003 (0 - 0.003)	0.012 ± 0.012 (0.001 - 0.035)
Biscay Gulf	0.006 ± 0.006 (0 - 0.012)	0.007 ± 0.006 (0 - 0.018)	-	0.003 ± 0.003 (0 - 0.008)	0.011 ± 0.010 (0 - 0.03)
western Mediterranean	0.018 ± 0.012 (0 - 0.041)	0.008 ± 0.007 (0 - 0.014)	0.016 ± 0.015 (0 - 0.045)	-	0.259 ± 0.024 (0.012 - 0.306)
eastern Mediterranean	0.006 ± 0.006 (0 - 0.012)	0.007 ± 0.007 (0 - 0.013)	0.018 ± 0.017 (0 - 0.051)	0.003 ± 0.003 (0 - 0.008)	-

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717 **Figure 1.** Regional sites of striped dolphin samples showing local populations and pooled sample set
718 (dashed circles) used for analyses; WM (western Mediterranean) and EM (eastern Mediterranean).
719 Sampling locations: northern Scotland (SC), south-east of Ireland (IR), Biscay Gulf, western France
720 (BG), Gibraltar Strait (GS), Valencia, eastern Spain (VL), Strait of Sicily (SS), Ionian Sea, western
721 Greece (IO), Korinthis Gulf, central Greece (KG) and Israel (IS).

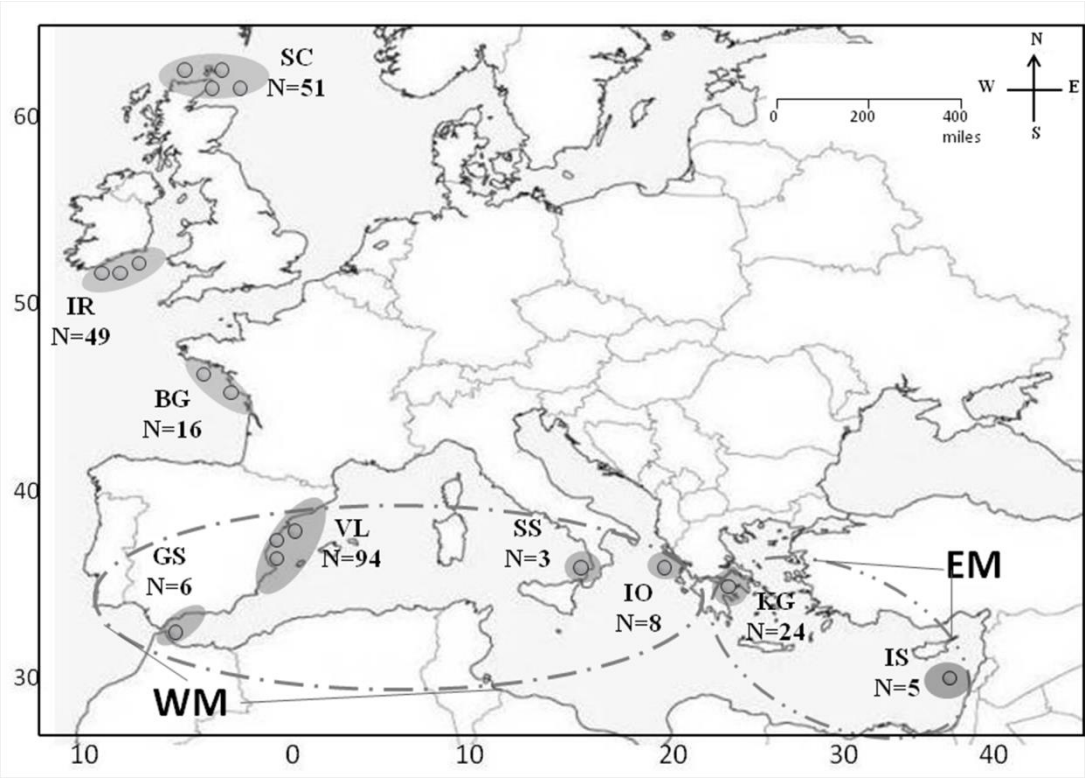
722
723 **Figure 2.** Factorial correspondence analysis (FCA) of striped dolphin population multilocus scores
724 computed using GENETIX. Multilocus scores are computed in the bivariate space defined by the first
725 two factorial components (SC: Scotland, IR: Ireland, BG: Biscay Gulf, GS: Gibraltar Strait, VL:
726 Valencia, SS: Strait of Sicily, IO: Ionian Sea, KG: Korinthis Gulf, IS: Israel). Lines show
727 nominal distinctions across the east/west and north/south axes.

728
729 **Figure 3.** Circos plots of source-sink migration dynamics for striped dolphin populations as
730 implemented in R platform (3.2.3). Plot corresponds to contemporary migration directionality
731 (using BAYESASS software). Width of migration curves indicates amount of migration according to
732 the scale provided (in units of the proportion of migrants per generation).

733
734 **Figure 4.** a) Logistic regression showing relative support for different scenarios for striped dolphin
735 population ancestry (see Fig. S1a in Appendix S2). Scenarios with support greater than zero are
736 shown. b) Illustration of the best supported scenario, scenario 8. Na = ancestral population, EM =
737 eastern Med, WM = western Med, IR = Ireland, SC = Scotland.

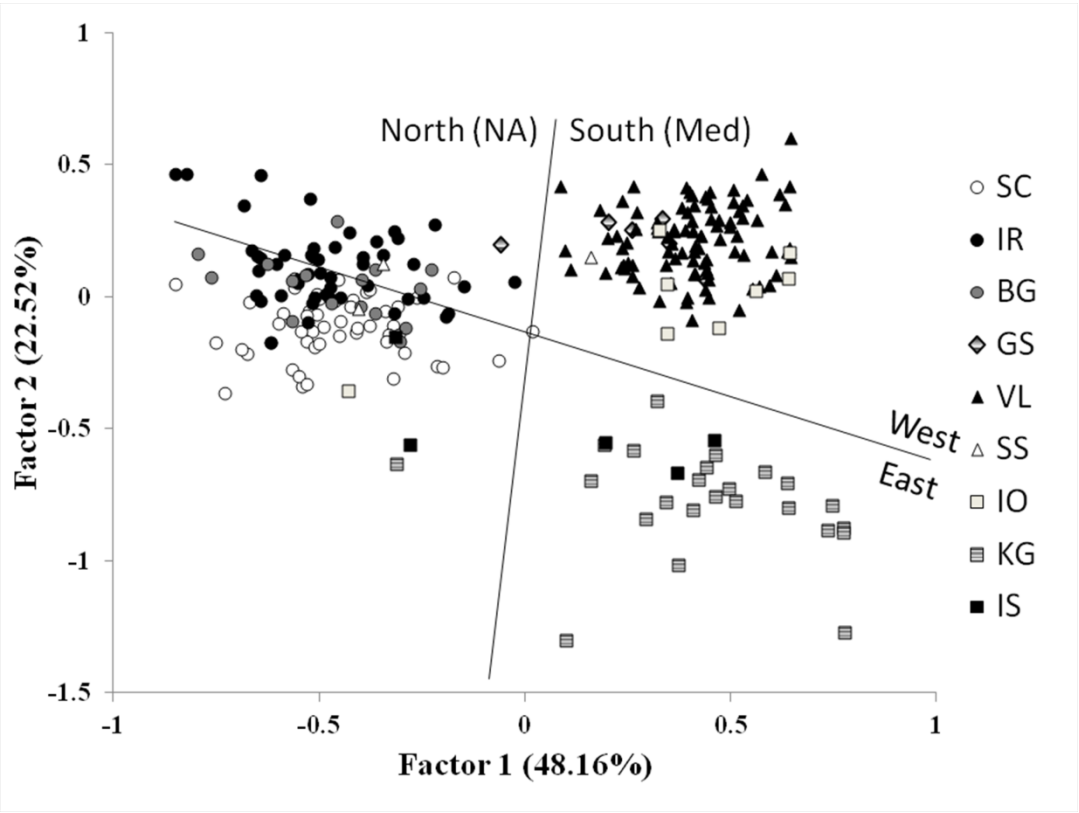
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740 Figure 1



748 Figure 2

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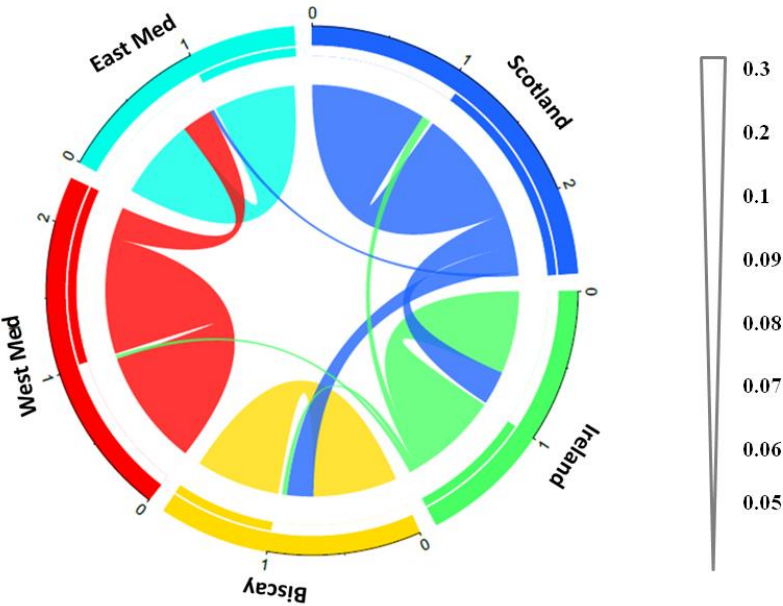
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762 Figure 3

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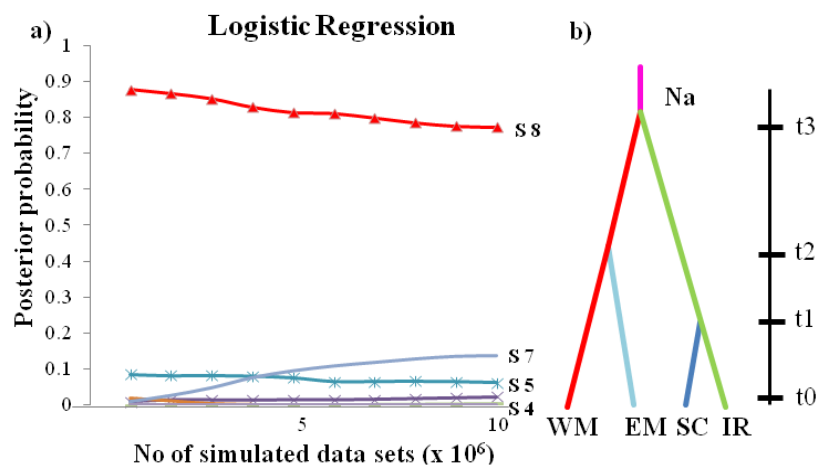
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767 Figure 4

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